NOTES AND LITERATURE

Orthogenetic Evolution in Pigeons. Posthumous works of C. O. Whitman, edited by OSCAR RIDDLE. Publication No. 257, Carnegie Inst., Wash. 3 quarto vols. with numerous colored plates and figures. 1919.

In the opening sentence of volume 1 of this notable publication, Whitman says "Progress in science is better indicated by the viewpoints we attain than by massive accumulation of facts." The viewpoint which Whitman himself attained and beyond which he saw no reason for advancing is that of "orthogenesis." His persistent industry also accumulated a mass of facts rarely surpassed in amount concerning variation in a single group of related organisms, the pigeons of the world.

The enormous task of setting these facts in order so as to illustrate his viewpoint, he was unable to accomplish. Death overtook him while he was still busy accumulating facts. But he was fortunate in having a loving pupil willing to devote his life, if necessary, to rescuing from oblivion the work and words of his beloved master. Few literary or scientific executors have shown such self-forgetting devotion or have seen it crowned with such success. Whatever we, living in a period of rapid advance in biology, think at present concerning the value of Whitman's viewpoint, there can be no doubt that Riddle has preserved it permanently, so that no one will be at a loss to know what Whitman's ideas were about the factors of evolution, or on what data they rested.

Whitman took as the point of departure in his pigeon studies, the plumage pattern of the wild rock-pigeon, *Columba livia,* made familiar to everyone by Darwin's use of it in his writings on evolution. Darwin supposed that the wild rock-pigeon of a slate blue color and with two black wingbars was the original form from which all varieties of domestic pigeons had originated through variation and selection. He showed that domestic varieties when intercrossed frequently revert to this wild type and he uses the manifold variation of domestic pigeons as a capital illustration of evolution through descent with modification. Whitman, in the true spirit of science which seeks to "try all things and hold fast [only] that which is good," made inde-

pendent studies of wild rock-pigeons obtained from the "Caves of Cromarty, Scotland." He found that not all the wild pigeons of this locality are of the simple two-wing-bar type, but that part of them show a different pattern known as "chequered." In these also the two black wing-bars can be observed, but they are rendered less conspicuous by the occurrence of other black spots scattered over other parts of the wing, giving the whole a chequered appearance. The wing-bars are due to the occurrence of a black spot on the tip or below the tip of each of two rows of feathers that lie across the wing when it is folded. In chequered birds other rows of feathers bear spots but the spots fall less regularly and obviously into rows, so that the pattern is more like that of a chequer-board. Further in young birds Whitman observed that practically all the wing feathers may bear spots, although in the later plumage some of the spots may disappear. He concluded that *this* condition was the primitive one, rather than the two-wing-bar type which Darwin regarded as primitive. This conclusion seems well founded since the chequered type is thus seen to be less specialized in form and earlier in ontogeny. So far Whitman's work supported Darwin's general evolutionary ideas, merely improving a detail in one of his illustrations, and showing that there still exists among wild pigeons a pattern yet more primitive than the one which Darwin had taken as the point of evolutionary departure. But Whitman now extended his investigations to other species of pigeons and finally to those of the entire world to see if he could work out more fully the evolutionary history of plumage patterns in the group. As a result of these studies he reached conclusions which did not enter into Darwin's scheme of evolution. The most important of these is known by the name of "orthogenesis." This is the idea that evolution through natural selection does not result simply from the selection of chance variations, that variations do not occur in *all* directions but only in particular directions in *straight lines* from the point of departure, hence the name *orthogenesis*. Whitman's study of the plumage patterns of pigeons is probably the most extensive, as it is the most recent, of the studies of a group of animals made in the light of this principle, but to the general body of biologists free from bias for any particular theory it will scarcely be more convincing than its predecessors. It is possible to arrange any group of related organisms in a graded series and to assume that they have been evolved by orderly development, from one end of the series (either end) to the other;

but this is no proof that such has actually been the historic method by which the series has arisen. It may actually have started in the middle and worked both ways, or in several directions. Only a study of contemporaneous genetic variation can show what the method of evolution is. Color variation in mammals is not unlike that of birds. We might arrange the color varieties of any species of mammal or group of mammals in a linear series and assume logically enough that evolution had progressed from the darkest to the lightest form in orderly manner, or *vice versa*, yet the study of contemporaneous variation shows that this is not the case. A wild species, like the gray rabbit or the brown rat, undergoes sporadically genetic variations ("mutations") some of which are lighter, some darker than the parental form. They have no relation to each other as to the order, time, or place of their appearance, so far as we can discover. Breeding evidence shows that they are genetically independent one of another.

As an alternative to the hypothesis of orthogenesis in variation, the mutation theory of DeVries received much critical consideration in Whitman's writings. The lateness of publication of much of this is to be regretted. Discussions which might have been helpful a few years ago are now quite superfluous and out of date in the light of critical experimental evidence since produced.

Mutation has practically ceased to be considered as a hypothetical method of the immediate and direct origin of species. Even as regards the origin of characters, mutation is no longer supposed to be a simple process. Whitman maintains with entire correctness that "unit-characters" often have small beginnings and may later be gradually increased by systematic selection. Frizzling of the feathers in pigeons and fowls is an example cited by him. He says, p. 151:

> Minute frills may occur in one or two feathers only, and they may occur in any number, or in all of the feathers. . . . The full character is reached, not by a jump, but by a process of modification, carried farther and farther, from the initial starting point. . . . It is well known that characters often disappear by degrees, not all at once. In crossing species we rarely find the hybrid with *pure* characters. A character may be halved, quartered, etc., to any fractional part of the original.

In passages such as these Whitman clearly shows that the muta-

tion theory as held at that time was untenable when applied either to the origin of species or to the origin of characters. What has since happened is that the mutation theory has been frankly abandoned as applied to such origins and is now limited to the origin of factors or genes. It is recognized that characters may change progressively and permanently (just as Whitman believed they did) under the guidance of selection. The agency of such change is now supposed to be modifying or multiple factors, so numerous as singly almost to baffle detection and so frequently coming and going that gradual modification of characters in a desired direction is not difficult. This is the residuum of truth which underlay the mutation theory as Whitman knew it and attacked it. In this marvellously modified form, he would probably not have attacked the theory at all.

Volume 2 deals chiefly with inheritance, sex, and color in hybrids of wild species of pigeons. An enormous amount of experimental data is here recorded, and scattered notes, briefs for lectures, etc., have been brought together by the editor, dealing with such general topics as heredity, Mendelism, sex determination and the like. As regards the hybrids, only F_1 individuals were produced, for Whitman says, p. 3,

> In the case of the wild species of pigeons, of which there are nearly 500, crosses are very often infertile, and fertile hybrids are so rare that Darwin could not find a single well-ascertained instance of hybrids between two true species of pigeons being fertile *inter se,* or even when crossed with one of their pure parents. The records since Darwin's time have not furnished the instance he vainly sought for.

Now every one to-day realizes that the F_2 or second hybrid generation is all important for understanding or interpreting heredity. Whitman accordingly, notwithstanding the boasted superiority as genetic material of the pure species with which he worked, since he was unable to produce in any case a second generation of hybrid birds, had no adequate basis for discussing heredity in his hybrids, and no adequate basis for criticizing Mendelism which is revealed only in the F_2 generation. One characteristic of the large number of sterile F_1 hybrid birds which Whitman produced is noteworthy. Their characters were in nearly all cases blends or intermediates between those of the respective parents. So long as doubt remained as to what the significance of blending is, whether it is essentially different in nature from Mendelian inheritance, Whitman thought rightly

that he had grounds for questioning the universality of Mendelian inheritance. But strong evidence has now been produced that blending inheritance is the regular outcome of crosses involving multiple factorial differences. F_2 in such cases shows increased variability with occasional segregation of the extreme parental types, and in F_3 and F_4 such segregation becomes more common. Had Whitman been able to raise F_2 and F_3 generations, he would undoubtedly have been convinced, contrary to his expectations, as some of us have been, that blending inheritance finds adequate explanation in multiple factor Mendelian inheritance. It is true that Whitman's records of hybrid birds reveal sex-linked inheritance, but these records did not suffice for its discovery, which fell only to those experimenters who worked with the despised "domestic breeds." The most valuable part of the work recorded in this volume is probably the basis which it afforded for experiments on quantitative factors entering into the development and expression of sex, if not its actual determination. This work is due largely to the pupil and editor, Riddle, though he generously brings the name of the master to the front in dealing with the subject. These results have been dealt with more fully in other publications by Riddle and need not here be reviewed.

Volume 3 deals with very different subject matter from that contained in Volumes 1 and 2, viz., the behavior of pigeons. Here is subject matter for the trained animal psychologist and Dr. Riddle felt constrained to call in a competent psychologist to edit this portion of Whitman's writings. Professor H. A. Carr has rendered this important service in a highly acceptable manner. That a single biologist should be able to do distinguished work in two fields so distinct as genetics and animal behavior shows the breadth of Whitman's capacities and interests. The reviewer is unable to deal critically with the contents of Volume 3, but hazards the suggestion that it contains material of very great interest and of permanent value not only to the psychologist but also to the naturalist, the one who is interested in animals as animals rather than as examples and products of one evolutionary process or another.

It is much to be regretted that Professor Whitman was unable himself fully to develop and round out the field of work here so ably outlined and in part explored.

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